

## THE MEASUREMENT OF ADULT MOSQUITO POPULATION CHANGES—SOME CONSIDERATIONS<sup>1</sup>

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**ABSTRACT.** Day-to-day changes in adult mosquito populations are difficult to measure due to the interactions between specific mosquito behavior, environmental influences upon behavior, and the mode of operation of the sampling technique. Mosquito responses to terrain features and various meteorological factors are briefly summarized with the object of improving our understanding of the samples provided by several classes of sampling techniques. The two major environmental influences upon the composition of a sample are the terrain features and several meteorological factors. As each sampling site is unique, a sample provides little direct information of the numbers of mosquitoes within the much broader area it is supposed to represent but it can reflect population changes at the site. However, the population changes usually are masked by meteorological effects upon flight activity. Data from Florida field studies were utilized to adjust trap catches to compensate for meteorological conditions during the catch period to provide more standard samples.

### INTRODUCTION

The basis of any sampling program is the collection of representative samples. A mosquito sampling program consists of a program design, data collection, and statistical analysis. However, data analysis is only as informative as the validity of the samples. Particularly when adult mosquitoes must be controlled, an accurate measurement of day-to-day population changes becomes of primary importance. Emphasizing Florida mosquitoes, this paper will examine the relationships among mosquito behavior, the influence of the environment upon behavior, and the mode of operation of the sampling technique upon the numbers and composition of the catch. The object is not to present a review of these topics, but a synthesis, whereby the representativeness of field samples may be improved. Only sufficient information on mosquito behavior and the effects of environmental factors upon flight activity will be presented so as to provide a basis for the objective.

Mosquitoes occupy a wide range of climates and habitats and in consequence exhibit widely differing behaviors. As it is impractical to address all behaviors, this paper will be limited to the most widespread—those species that rest during the day and fly at night. Only female behavior will be addressed.

### BEHAVIOR AND THE ENVIRONMENT

The interaction between the innate behavior of mosquitoes and the environment is the basis of mosquito ecology. Adult mosquitoes are ex-

posed to a harsher environment than as larvae. As compensation, their mobility enables them to avoid unsatisfactory conditions and to travel long distances in search of their needs.

**FLIGHT.** Mosquito flights may be classified as migratory, appetential or consumatory. Migratory flight lacks an objective and does not meet any individual need (Provost 1952, 1953). Migratory flights, although emigratory may be more accurate as there is no return flight, are performed only by newly emerged adults. These adults, meteorological conditions permitting, depart from the breeding area, usually at dusk, when about 6 to 10 hr of age. Except that the older mosquitoes may imbibe nectar before departing (Haeger 1955), migrants lack physiological needs and are unresponsive to most environmental stimuli. For example, migrant *Aedes taeniorhynchus* (Wiedemann) readily cross large bodies of open water which older females will not (Provost 1957). The migratory flight is upwind at velocities less than 1 meter per second (mps) but downwind at higher velocities (Haeger 1960). As the direction of the migration is determined by wind conditions at the time of departure and its duration limited by the mosquitoes' energy reserves and meteorological conditions, the destination of a brood is primarily fortuitous. Migratory flights have not been identified in most mosquito species.

Appetential flight (Provost 1952, 1953) occurs in adult mosquitoes over 24 hr of age and is undertaken in response to a physiological stimulus. Environmental conditions permitting, a resting female mosquito in need of a blood meal, an oviposition site, a better resting place, or if for any reason is unsatisfied, will embark upon an appetential, or searching flight. During the flight her appropriate sense organs, whether olfactory, visual, thermal, auditory, or

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humidity receptors, will be alert for a cue that indicates the presence of her objective. The flight is probably interrupted frequently by rest periods, as the energy reserves of wild mosquitoes are low (Magnarelli 1983, Magnarelli and Andreadis 1984). The appetential flight ends the moment such a cue is encountered.

The subsequent flight to her goal is the target (Haskell 1966) or consumatory flight. It is direct and brief, since visual and biochemical cues do not operate over long distances. If the cue encountered was olfactory a direct upwind flight is conducted (Gillies and Wilkes 1972, 1974) until other cues, visual perception, movement or thermal, enable the female to locate her goal more precisely. Consumatory flights may occur without the preceding appetential flight; an example would be the biting that occurs when a host enters mosquito daytime resting sites.

Since the migratory flight occurs only during the first night and the lengths of the consumatory flights are necessarily short (Gillies and Wilkes 1972, 1974), almost all of a female's flight activity during her life is occupied in appetential flights.

**HABITATS.** Resting sites serve as refuges from adverse environmental conditions, as voluntary flights will be performed only if environmental factors permit. Females of some species use the same habitat for all activities, whereas other females rest and fly in dissimilar areas. During the daylight hours, species such as *Psorophora columbiae* (Dyar and Knab), *Psorophora ciliata* (Fabricius) and *Aedes sollicitans* (Walker) commonly rest among grasses in areas exposed to the sun (Bidlingmayer 1971). Most species, however, select cool and shady locations, moist woodland being ideal. Although at night the searching flights of a few species, such as *Culiseta melanura* (Coquillett) and *Culex nigripalpus* Theobald, are also conducted principally in wooded areas, many species, e.g., *Aedes vexans* (Meigen), *Ae. taeniorhynchus*, *Anopheles crucians* Wiedemann, and *Coquillettidia perturbans* (Walker), prefer open areas. Consequently, mosquitoes form 3 fairly distinct groups: the field species, which both rest and fly in open areas, the woodland species, which rest and fly in woodland, and the commuter species (the largest group), which rest in woodland during the day but each evening fly outward into open areas and return at dawn (Bidlingmayer and Hem 1981). Nevertheless, no species is ever confined to a particular habitat; small numbers of *Cs. melanura* are taken at long distances from the nearest woodland; a few *Ps. ciliata* are captured deep within wooded swamps. In varying numbers, adult mosquitoes occur everywhere.

Figure 1 outlines the principal factors that comprise an adult mosquito's environment. These are: physiological needs, such as energy and protein sources and oviposition sites, suitable habitats for day and night activities, the terrain features, as vegetation types, water bodies, and the effects of human activities, and the various meteorological factors that release or suppress flight activity. Physiological and habitat needs stimulate appetential and consumatory flights; terrain features and meteorological factors determine the location, time, direction and extent of these flights. Therefore, the effects of terrain features and meteorological conditions upon flight behavior, and consequently, upon sampling, needs close examination.

**TERRAIN FEATURES.** With some exceptions, such as extensive monocultures, mosquito habitats are not uniform. The terrain may exhibit variation in height and density of vegetation, land elevations, soil moisture, types of surface water, and types of human activities. From different points within a habitat, distances to nectar and blood sources and to oviposition sites are unequal. These features are arranged in unique combinations and patterns. Even within a well-defined habitat, the mosquito inhabitants at different locations are not exposed to exactly the same physical environment. Mosquitoes respond to slight physical differences and numbers vary within each habitat.

**METEOROLOGICAL FACTORS.** The principal meteorological factors affecting flight activity are illumination, temperature, humidity, and wind.

In Florida, truck trap and suction trap catches revealed that most species possessed a bimodal pattern of flight activity during the night, with the largest peak occurring soon after sunset and the smaller peak just prior to dawn (Bidlingmayer 1974). These are times of rapidly changing illumination levels. Female mosquitoes needing to perform appetential flights and representing apparently all physiological stages (Edman and Bidlingmayer 1969, Bidlingmayer 1974), are released into flight at these times. As each individual mosquito has its own upper and lower illumination thresholds for flight, the crepuscular peaks of flight activity are due to the distribution of individual thresholds. Total flight activity declines as light levels fall below or rise above the mean preferred intensity. During the dark hours of the night flight activity is greatly reduced and composed principally of blood-seeking females. However, any increase in illumination levels, as from moonlight, permits increased flight activity in which even some blood-fed or gravid

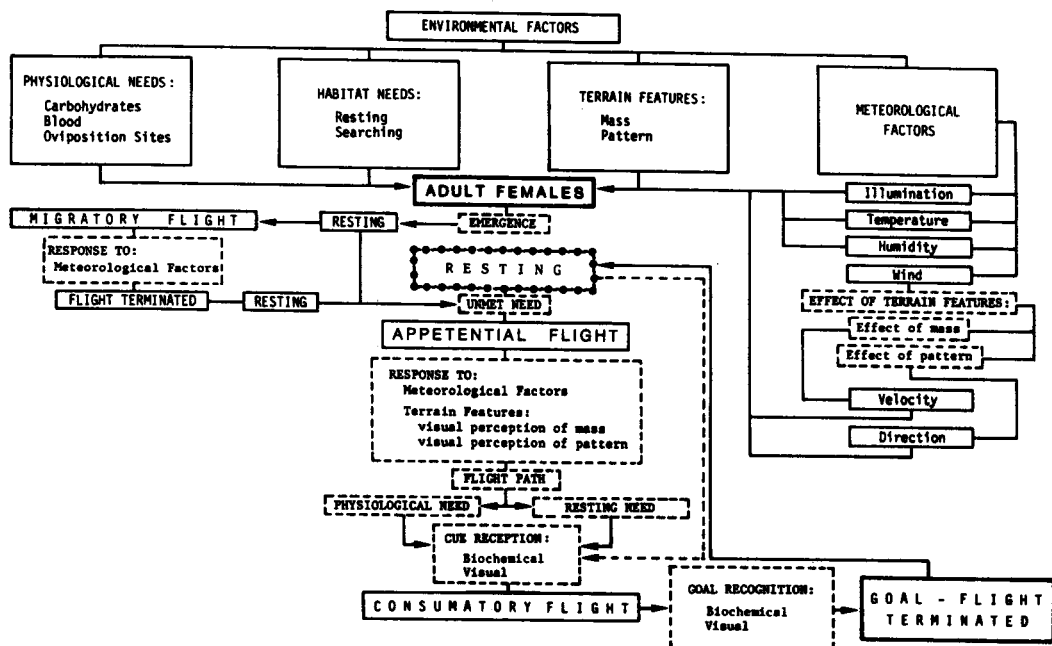


Fig. 1. Principal environmental factors that affect the time, amount, and course of flights by female mosquitoes. Also shown is the alternation of resting periods with appetential and consummatory flights.

females participate (Bidlingmayer 1974). Thus, illumination changes between sunset and dawn alternately stimulates and suppresses flight activity and changes the physiological composition of the aerial population.

Once temperatures have risen above an individual insect's minimum temperature threshold for flight, higher temperatures do not further affect its flight (Taylor 1963). The increasing catches that accompany rising temperatures are due to differences in individual temperature thresholds. Consequently, at least within the ranges experienced during the night, there are lower and upper temperature thresholds at which the first and last individuals, respectively, of a population may engage in flight (Rudolfs 1925). In contrast to the upper illumination threshold which terminates appetential flight, temperatures greater than the upper temperature threshold neither inhibit nor increase mosquito flight activity.

Adult mosquitoes in northern latitudes are active at lower temperatures than those in warmer climates. Gjullin et al. (1961) and Corbet and Danks (1973) found tundra mosquitoes were not inactivated until about 5°C. For active dispersal of *Aedes* mosquitoes, the mean nightly temperature in southern Manitoba should be > 15°C (Brust 1980). Grimstad and DeFoliart (1975) did not find nectar feeding at temperatures < 10°C in Wisconsin. *Culex tarsalis*

Coquillett in California began flight at 13°C and were biting at 15°C (Bailey et al. 1965). In Florida, Bradley and McNeel (1935) reported that temperatures < 21°C and Bidlingmayer (1974) found that temperatures < 19°C, reduced catches.

Mosquitoes also appear to have lower and upper humidity thresholds, although these are poorly delineated. Rudolfs (1923, 1925) found that catches of *Ae. sollicitans* and *Culex pipiens* Linnaeus were reduced when relative humidities exceeded 85% and 97%, respectively. Peak catches of *Ae. vexans* in New Jersey light traps occurred on nights when the relative humidity was between 60% and 90% (Platt et al. 1958). Wright and Knight (1966) reported that *Ae. vexans* and *Ae. trivittatus* Coquillett were active between 32% and 98% RH while Grimstad and DeFoliart (1975) found flight activity for several northern species was suppressed below 48% RH and required > 70% for usual activity. Above 97% RH, flight activity was suppressed. In Florida, humidity thresholds have not been reported. Dow and Gerrish (1970) found a 3.6% increase in day-to-day changes in bait trap catches of *Cx. nigripalpus* with each 1% increase in evening relative humidities. Bidlingmayer (1974) compared evening and dawn catches of *Cx. nigripalpus* from several traps with relative humidities at these times and found the larger dawn catches

were correlated with the greatest increases in humidity. High correlations were also found between New Jersey light trap catches of *Cx. nigripalpus*, *An. crucians*, *Deinocerites cancer* Theobald and the percent relative humidity 1 hr after sunset by Provost (1974).

Wind has 2 components, velocity and direction. Velocity is reduced by friction as it flows over or about obstacles, friction increasing with increasing numbers and dimensions of the physical features of the terrain (= "mass" in Fig. 1). The various terrain features, due to their placement relative to each other and their angle to the wind, affect both wind velocity and direction. Direction changes may be as great as 180°, as when after surmounting a perpendicular obstacle such as a hedge or row of trees, a backflow of air is created close to the ground on the leeward side (Lewis and Dibley 1970). Except during short bursts, mosquito cruising flight speeds are usually less than 1 meter per second (mps) and flight activity is noticeably reduced if winds exceed flight speeds (Grimstad and DeFoliart 1975 (1.5 mps), Gillies and Wilkes 1981 (0.5–1.4 mps), Snow 1977 (0.5–1.5 mps), 1980 (1.2 mps), 1982 (0.5 mps), Service 1980 (0.8 mps), Hocking 1953 (1.1–1.6 mps), Wright and Knight 1966 (0.9 mps), Gjullin et al. 1961 (0.9 mps), Bidlingmayer 1967 (0.5 mps), 1974 (0.7 mps), Bidlingmayer et al. 1985 (0.4 mps).

Within uniform habitats, as in the central areas of large fields, there is usually little variability between sites for the various meteorological factors. If a forest surrounds a field, illumination, temperature and humidity values at locations near the forest edge will be much less affected than will wind values. However, the terrain often consists of irregular patterns of shrubs and trees, houses and lots, forests and water. Wind velocities and wind directions at different sampling locations in such areas will be much more variable than other weather factors as temperature and humidity.

The responses of the mosquito to the environment while in pursuit of its physiological and habitat requirements leads to the formation of more or less well defined flight paths (Bidlingmayer 1967). These are a major feature of appetential flights.

**FLIGHT PATHS.** During appetential flights, the 2 principal factors determining the aerial routes traveled by mosquitoes are wind direction and visual orientation.

In regard to wind direction, provided velocities do not exceed flight speeds, mosquitoes basically fly upwind (Klassen and Hocking 1964, Haskell 1966, Klassen 1968). This is due to the optomotor response which requires

ground images, i.e., dark and light patterns, to pass beneath an insect's eyes from front to rear at particular frequencies (Kennedy 1940, David 1982). Because the flicker rate of the images must remain within a limited range, insects tend to fly faster as air velocities increase. More energy is consumed and presumably on windy nights less time can be spent in flight. As wind velocities increase with height above the ground, a boundary layer exists which is defined as the air between the ground and the height at which wind speeds exceed flight speeds (Taylor 1974). Above the boundary layer only downwind flight can occur. The effects of differing wind velocities upon the direction and elevation of mosquito flight have been discussed by Klassen and Hocking (1964), Klassen (1968) and Snow (1976).

Mosquitoes have well-developed eyes which are sensitive to illumination levels less than starlight (Muirhead-Thomson 1940). Visual acuity, even at low illumination levels, is good (Hocking 1964). Suction traps painted black captured larger numbers than gray traps and gray traps captured larger numbers than transparent traps (Bidlingmayer and Hem 1979). Presumably any visible object whose dimensions fall within an acceptable range, whether a trap, a bush, an animal, or other visible feature of the terrain, may serve as a visual target.

Attraction to visible objects requires mosquitoes to make a choice when more than one object is in view. When 4 suction traps were spaced 15 m apart in a row in a field, traps at the ends of the row captured larger numbers than the traps within the row; when 16 traps were placed 15 m apart in a 4 × 4 grid, traps at the corners of the grid captured the greatest numbers, traps along the side fewer, and traps in the center of the grid captured the least numbers (Bidlingmayer and Hem 1980). Mosquitoes were most strongly attracted to the traps with the smallest number of adjacent traps. When several visual targets are present, these compete for the mosquitoes' attention and the target with the least cluttered background is most conspicuous. It was estimated that had only a single trap been placed in the field, 5 times as many mosquitoes would have been taken as by a trap surrounded by 4 traps. Further analysis of the catch ratios between traps indicated mosquitoes were attracted to these particular traps from an average distance of 15 to 20 m. Thus, in most habitats, flying mosquitoes would be within range of several visual targets at all times.

Although attracted to visible objects from a distance, actual contact is avoided (Kellogg and Wright 1962). The closeness of approach to an

object before changing direction differed among species (Bidlingmayer and Hem 1979). *Culex nigripalpus* approached suction traps more closely before changing direction than did *Ae. taeniorhynchus* or *Anopheles atropos* Dyar and Knab. *Culiseta melanura* and *Cx. nigripalpus* approached a vertical barrier more closely than did *Ps. columbiae* or *An. crucians* (Bidlingmayer 1971, 1975). Consequently, the species composition of the air space near a visible object changes with increasing distances from the object.

When traps were placed at different elevations on a tower, Snow (1977, 1979, 1982) reported mosquitoes were visually attracted to traps high on the tower. Woodland and commuter species appear to orient visually to high horizons (Gillies and Wilkes 1974, Bidlingmayer and Hem 1981). In a field the numbers of field species, (i.e., *Ps. columbiae* and *Ps. ciliata*), captured at different distances from the edge of a woods were similar. However, the numbers of commuter species (*Ae. vexans*, *An. crucians*, *Culex (Melanoconion)*) and woodland species (*Cx. nigripalpus*, *Cs. melanura*) declined with increasing distances from the woods. Apparently females of the latter groups limit their nocturnal forays into the field, perhaps by orienting to a high horizon, so that at dawn a suitable resting site is nearby.

Upon encountering a physical or visual barrier, the usual response of insects is to fly over it (Johnson 1969, Service 1974, Bidlingmayer 1971, 1975, Gillies and Wilkes 1978, Bidlingmayer and Hem 1979). Mosquitoes may, however, also follow along hedgerows and high borders of fields (Giglioli 1965, Klassen 1968, Nasci 1982). These flights may also be guided by the effect of a horizon.

It is probable that the visual responses of mosquitoes during appetential flight differ from those made during consumatory flight principally in degree. The former are responses to coarser terrain features which serve to direct the female toward the proper habitat—which presumably increases the probability of encountering her objective. The latter would consist of visual response to smaller objects and to movement.

In summary, when wind velocities are low, the appetential flight of female mosquitoes is basically upwind; flight was mostly upwind even on nights when air movement was too low to be measured (Bidlingmayer et al. 1985). However, visual attraction toward conspicuous objects causes females to deviate from a strict upwind orientation. At close range, the visual target will fill their field of view and thereby lose its identity. The female is then compelled to select

another target, the most conspicuous being selected. As different visual targets successively come into view, the females orient toward first one and then the next. Consequently, anastomosing streams of females are formed as females with similar objectives make similar responses. The location of these flight paths will vary from night to night, or even during the same night, with changes in wind direction. Therefore, a trap may lie within a flight stream on one occasion—and take large catches—but not on the next. Consequently, catches from fixed traps are quite variable. Because of this variability, catches of *Ae. taeniorhynchus* in suction traps operated during full moon appeared to have increased only two-fold above new moon catches whereas catches from the truck trap increased 10-fold.

If flight occurs when wind velocities exceed flight speeds, the mosquito ascends and flies downwind, as the flicker rate is again within an acceptable range (Klassen and Hocking 1964, Klassen 1968). After descent, upwind flights are renewed if low velocities are found, as in the lee of a windbreak or close to the earth. While the number and duration of appetential flights differ between species, their total length often results in dispersals of approximately 3.2 km (2 miles) nightly. Mosquitoes taken while making consumatory flights usually represent the terminus of multiple appetential flights.

The resting, appetential flight consumatory flight, cycle is shown in Fig. 1. After emergence, the female normally rests for several hours. If a latent migrant, provided its energy reserves are adequate and meteorological conditions are favorable—a migratory flight occurs which continues until reserves become low or meteorological conditions are inhibiting. Subsequently, when the first need arises, the first appetential flight is undertaken. Visual responses to terrain features and meteorological influences now guide the flight along a flight path. The route of the path will differ whether the unmet need was stimulated internally by a physiological need or externally, as by unfavorable environmental factors. When a biochemical or visual cue indicate the presence of the goal, the consumatory flight begins. Nearing the goal, additional cues confirm its identity and exact location. Except for the initial migratory flight, nonmigratory females follow the same sequence of flight and resting activities.

Throughout their lives females will need resting sites, carbohydrates, vertebrate hosts, and oviposition sites, each of which successively stimulate the cycle of appetential and consumatory flights. However, satisfaction of a need is soon followed by a new need and a new

appetential flight. Near dawn the various nocturnal activities end with a search for daytime resting sites.

**SAMPLING TECHNIQUES**

Sampling equipment is constructed of wood, metal, and plastic and in operation possesses a high degree of mechanical reliability. The differences in catch composition found between sampling techniques are due primarily to differences in mosquito behavior. To be satisfactory, a technique's principle of operation must be in accord with some aspect of the behavior of the target species. A review of mosquito-sampling devices and techniques has been published by Service (1976).

The more frequently used traps and techniques employed to sample mosquitoes are listed in Fig. 2. The principal relationships between the different sampling techniques, mosquito activity at time of capture, and the physiological composition of the catch, are also shown. Resting mosquitoes are taken during the day when all segments of the population,

whether unfed, blood-fed, or gravid are at rest. Their proportions in the sample should be representative of the population. In many cases, the proportions of each physiological group in the sample do seem reasonable when compared with the observed duration of each stage during a gonotrophic cycle, particularly if an additional day or two are allowed for host-seeking and feeding. However, the proportions of the various physiological groups may be atypical if an unusual environment is present, such as abundant blood sources or extensive larval breeding sites. Probably all resting site populations reflect, to some degree, the local abundance or scarcity of various mosquito needs.

The numbers of resting mosquitoes captured from ground litter, which were taken during the daylight hours, were related to the amount of resting habitat. Where woodlands were extensive ground catches were small, even when nocturnal aerial catches were large (Bidingmayer 1974, cf Table 13). Conversely, where woodlands were small and widely scattered, ground catches were disproportionately large due to crowding into the limited areas

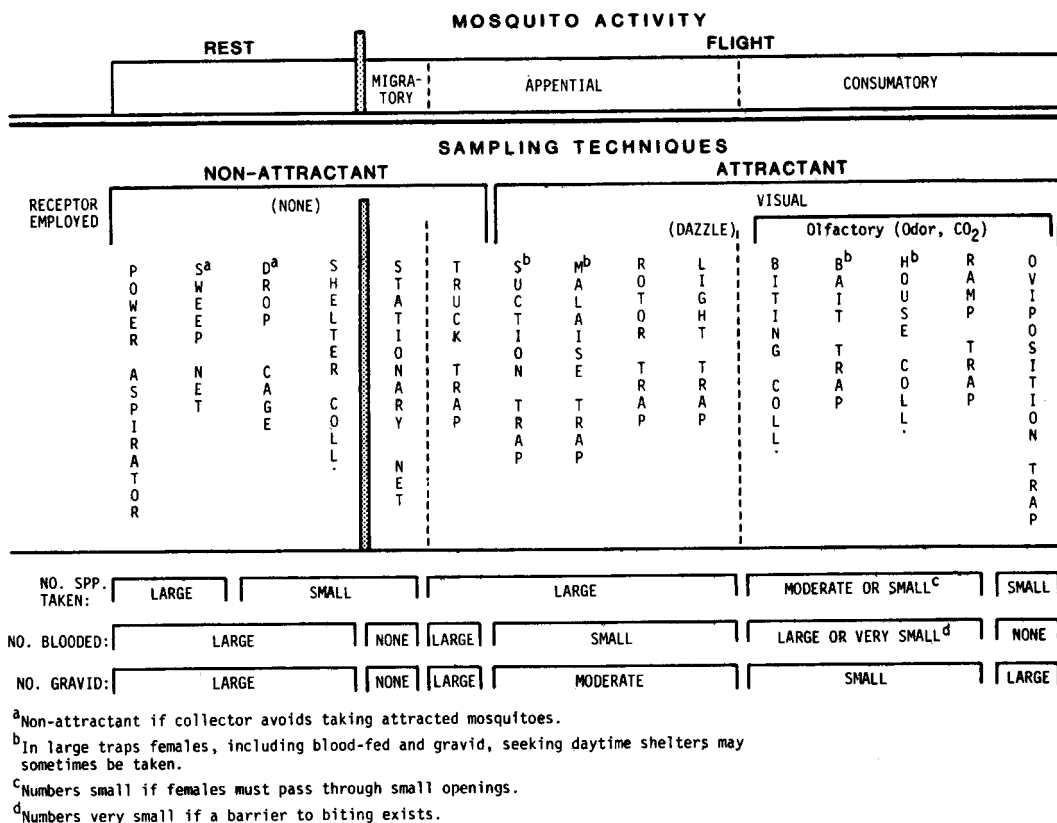


Fig. 2. Classification of adult mosquito sampling techniques by mosquito activity and receptors employed.

available. Since habitats are seldom uniform throughout, collections of ground-resting mosquitoes do not seem to be well suited to measure population changes. Rainfall, following a dry period, can greatly expand the areas within the habitat that are suitable for resting, and cause an immediate decrease in the numbers captured. During a dry period, it can be anticipated that population declines could be masked by increasing concentrations of mosquitoes in the shrinking areas of suitable resting habitat remaining. Collections of resting mosquitoes were most useful for sampling the physiological composition of a population.

Both power aspirator and sweep nets can be used to sample the many species of ground-resting mosquitoes. The first range in size from those mounted on a 4-wheel drive vehicle to hand-carried units powered by a small gasoline engine or 12-volt electric motor (Dietrick 1961, Bidlingmayer and Edman 1967, O'Meara and Edman 1975). Collections can be made in a variety of habitats, ranging from open pastures to brushy areas to woodlands and swamps. Sweep nets are difficult to use in some habitats and the sweeper may be an attractant. Drop cages (deZulueta 1950) sample only those species resting in open savannas and therefore the number of species taken is small.

Population changes in the small number of species that occupy natural and artificial shelters may be monitored by shelter collections, as the number of suitable shelters available is relatively constant. The numbers of mosquitoes present in a shelter will be related to both the abundance of shelters and also to the time of collection, as mosquitoes frequently move into and out of the shelter throughout the day.

Most techniques sample mosquitoes while in flight. Migratory flights have not, except immediately adjacent to the breeding area, been successfully sampled. Because migrants are unresponsive to terrain features, the adults fly into devices as simple as an open stationary net. Catches consist only of migrants, as non-migrants either do not enter the nets or readily escape (Nielsen 1960). The brief existence of these flights causes them to be unimportant to workers measuring mosquito populations.

Appetential flights must be sampled by techniques that capture mosquitoes while engaged in a searching flight, i.e., before a response to a consumatory cue occurs. However, as visual attraction to conspicuous objects is an integral part of appetential flights, catches made by immobile traps should be assumed to have a visual component.

Traps sampling appetential flights take a wide variety of species and large numbers may be captured (Fig. 2). Only the truck trap (Bid-

lingmayer 1966) samples appetential flights unaffected by visual responses to the trap. As mosquitoes are collected over a long distance, the catches are unaffected by the various shifts that occur in mosquito flight paths. As a result, there is less variability between replicate catches, e.g., the effect of moonlight upon flight activity was demonstrated after 1 year's work with a truck trap (Bidlingmayer 1964, 1974), whereas 3 years' work were required with a suction trap. The proportions of blood-fed and gravid females in truck trap collections were quite similar to those found in collections of resting mosquitoes, which attests to its low level of sampling bias. That the composition of the catches is not noticeably affected by the vehicle's headlights is evident from the very small numbers of these stages taken by the New Jersey light trap. Furthermore, in contrast to light traps, the largest mosquito catches were made during periods of full moon (Bidlingmayer 1964, 1967).

The suction trap, as presumably are all other visible objects, is a visual attractant. Its attractiveness will vary with its size, shape, color, and its placement in relation to competing visual attractants. As the closeness of approach to an object differs between species, changes in trap design or air flow will change its attractivity or the catching radius of the trap and thus the species composition of the catch. Suction traps, like other fixed traps, sample mostly the downwind population and the catches will be affected by changes in wind direction and the resulting shifts in mosquito flight paths. The proportions of blood-fed and gravid females found in suction trap collections were small, and much more similar to the even smaller proportions of these stages found in light and bait trap catches than to the proportions found in truck trap collections. Visual attraction to conspicuous objects is primarily a response of blood-seeking females. However, large numbers of blood-fed anophelines have been taken in suction traps during the morning twilight period, which clearly demonstrates the effect of mosquito behavior upon the composition of trap collections (Bidlingmayer 1974). It is possible these females were attempting to use the trap as a daytime shelter.

The Malaise trap (Breeland and Pickard 1965, Gunstream and Chew 1967) also functions as a visual attractant (Corbet and Danks 1973, Service 1977). Because of its design, the catch will consist of host-seeking and some shelter-seeking females. As females of some species pass through small openings less readily than others, the catch of these species will be reduced.

The motor and gear box of a rotor trap

would be visually conspicuous as the trap cannot be placed close to other objects due to the space requirements of the rotating nets. Whether female mosquitoes would also respond, by a consummatory flight, to the movement of the nets has not been investigated.

Although light traps have long been used to sample adult mosquitoes, little consensus exists regarding the meaning of the sample. By comparing catches obtained from a variety of sampling techniques under diverse conditions, our current knowledge of mosquito flight behavior supports the hypothesis presented by Robinson (1952) and Verheijen (1958). These authors assume that flight orientation requires visual control. Visual responses to the environment are necessary to enable the insect to maintain a horizontal position and to fly upwind. Controlled flight is possible because of light reflected by the environment, not light from the light source. Capture in light traps is effected by disoriented behavior, since mosquitoes have not had evolutionary experience with artificial light.

The brightness of a light source is inversely proportional to the square of its distance. Consequently, if a field of artificial light lies across a flight path, the mosquito enters an area of rapidly increasing illumination (Fig. 3). The area contains 3 zones: a zone of repulsion, wherein illumination levels are greater than the

female's preferred level and turning movements are the usual response; a zone of inhibition, where mosquito eyes begin to change from dark-adapted to daylight-adapted and which, if completed, causes insects to settle; and last, a dazzle zone in which, due to the mosquito's inability when close to the light source to perceive reflected light, visual contact with the environment is lost. A disoriented flight toward the light source follows, perhaps because the light is its only remaining visual reference point. The zones of repulsion and inhibition act as barrier zones and mosquitoes are not attracted to the light.

Artificial light does not supply any mosquito need and therefore light traps must be sampling appetential flight (Fig. 2). The efficiency of light traps is reduced when ambient illumination levels are high due to the greater amount of reflected light in the environment, which reduces the size of the dazzle zone. Catches consist almost entirely of host-seeking females, which may be, in part, a consequence of blood-fed and gravid females flying principally during twilight and on moonlit nights, times when light-trap efficiency is low (Bidingmayer 1974). Differences between species in "attractancy" to light are a function of each species' optimal level of nocturnal illumination. As woodland females fly at low illumination levels, the zones of repulsion and inhibition

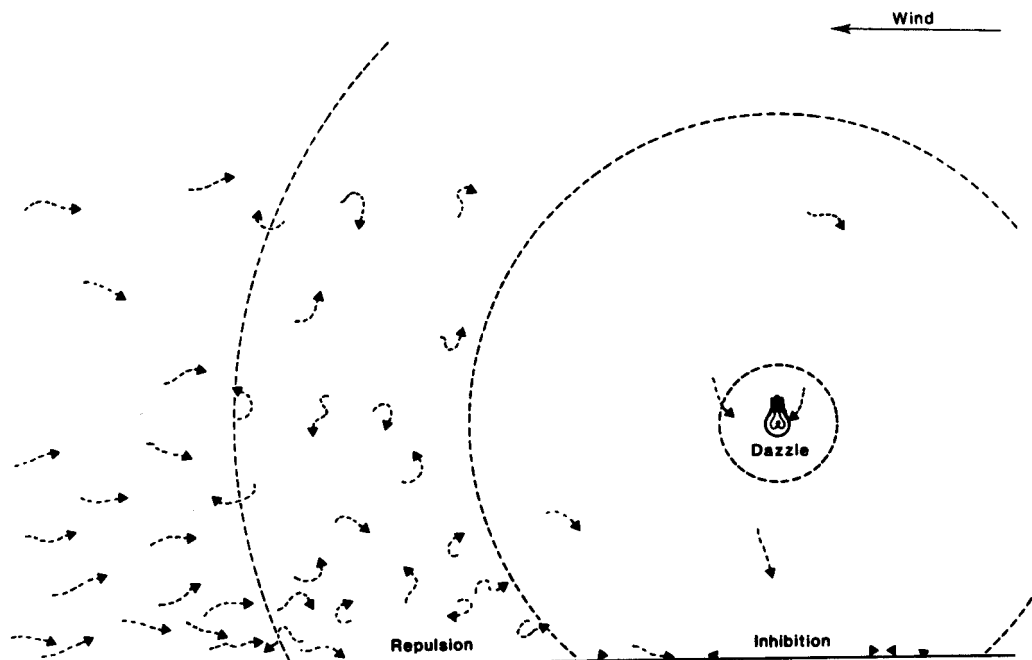


Fig. 3. The zones of repulsion, inhibition, and dazzle about an artificial source of light. For explanation, see text (Based on Robinson (1952) and Verheijen (1958).



about a New Jersey light trap will be wider than for commuter or field species. Consequently, a smaller proportion of woodland females than of commuter or field females will cross the barrier zones. For species with very low illumination requirements, light traps may actually take smaller numbers than the same traps without light (Reed 1959, Bidlingmayer 1967). However, if small battery-powered traps are used—providing a light of comparable intensity but lower power—the widths of the barrier zones would be reduced and these should now be crossed more readily by woodland females.

Knowledge of the physiological responses of insects to artificial light is still too limited to explain all light trap catches (Hsiao 1972). The indifferent success of light traps in Europe and Africa for mosquitoes is difficult to explain. For other examples: 1. Light traps, compared with truck, suction or bait trap catches, usually captured proportionately larger numbers of mosquitoes during the dawn period than during dusk. This suggests, despite during each period the same range of illumination levels, a differing physiological response to light at dusk and dawn. 2. Although all other sampling methods captured larger numbers of mosquitoes during moonlit periods, the New Jersey trap took fewer (Bidlingmayer 1974), the reduction in New Jersey trap numbers, however, being several times greater than the increase in other traps. Light traps, therefore, are more sensitive to ambient illumination levels than other traps. 3. Whether due to slower ground speeds or to more frequent rest periods, strong winds reduce mosquito catches in all traps. For light traps, a slower passage through the trap site would also lengthen the female's exposure to the light and thus increase the effectiveness of the barrier zones. In summary, light traps seem to be subject to little understood variables in addition to those that affect all sampling techniques. Although a field species, the numbers of *Ae. sollicitans* captured in light traps were very small compared with females of other field species. However, suction and bait traps also captured very small numbers (Bidlingmayer 1974). Only the truck trap captured large numbers, suggesting that *Ae. sollicitans* may fly at higher elevations than other species.

When animal odors and/or carbon dioxide are used as an attractant, host-seeking females are presented with a definite olfactory clue to their goal (Gillies and Wilkes 1969). Being wind-borne, the effectiveness of the olfactory plume will be affected by both terrain features, which disperses and thereby shortens the plume, and by wind. At higher wind velocities the plume is dispersed more rapidly than at low velocities (Wright 1958). Changes in wind di-

rection carry the plume into areas with differing mosquito densities. Furthermore, individual human and animal hosts may differ in attractiveness to mosquitoes. In addition to those terrain and meteorological factors that afflict all sampling methods, these variables affect the techniques that require a consumatory flight. It is common practice to use carbon dioxide with certain light traps. Such light trap collections, obviously, will also have been affected by the factors associated with the host attraction.

Hand catches of mosquitoes coming to feed during a fixed period of time have long been used to provide a measure of mosquito populations (Fig. 2). Because access to the host is unimpeded, the number of species taken is, while often less than in traps that sample appetential flight, quite large. However, females of some species are more wary and thus more difficult to capture than others. Mosquito temporal biting patterns during the diel vary greatly among species, and the numbers and species composition of the catch will reflect these behavioral differences.

To reduce human exposure and more easily extend the sampling time, animal or bird-baited traps have been designed, although these hosts cannot duplicate the frequency of blood feeding on man. The design of bait traps has 2 principal characteristics that affect the composition of their catches, viz., whether or not the blood-seeking female must pass between louvers or through a small opening to approach the bait, and whether the bait is subjected to, or protected from, female attack. Mosquito species differ in their readiness to pass through small apertures. Traps with this feature will take an appreciably smaller number of species than traps in which the approach to the bait is unimpeded. In those traps whose design does not utilize small entrances, capture is effected by intermittent suction, spring-loaded nets, or other means. Regardless of the mode of capture, baits may be either exposed to the females or protected behind fine screening; obviously, the presence of engorged females in the catch will be determined by this difference. When large bait traps, as bed-nets or stable traps, are used, some shelter-seeking mosquitoes will undoubtedly be captured.

House collections (Service 1977) have not been used in Florida, but houses used for this purpose are essentially large bait traps with human bait. When houses are of loose construction, the mosquitoes may enter through various openings. Windows may be fitted with ingress or egress baffles, or mosquitoes may be captured by hand or with the aid of space sprays, bed-nets or even small light traps. The species composition of the catch will depend

Table 1. Principal factors affecting the numbers and composition of collections of flying mosquitoes taken by various techniques.

	Non-attractant		Attractant								
	Stationary net	Truck trap	Suction trap	Malaise trap	Rotor trap	Light traps	Biting collections	Bait traps	House collections	Ramp trap	Oviposition trap
<b>FLIGHT</b>											
Migratory	x										
Appetential		x	x	x	x	x	x	x	x	x	x
Visual responses			x	x	x	x	x	x	x	x	?
Consumatory					?	x <sup>a</sup>	x	x	x	x <sup>a</sup>	x
Visual responses					?	x <sup>b</sup>	x	x	x	x <sup>a</sup>	x
Olfactory responses						x <sup>a</sup>	x	x	x	x <sup>a</sup>	x
<b>METEOROLOGICAL</b>											
Illumination	x	x	x	x	x	x	x	x	x	x	x
Temperature	x	x	x	x	x	x	x	x	x	x	x
Wind Velocity	x	x	x	x	x	x	x	x	x	x	x
Wind Direction	x		x	x	x	x	x	x	x	x	x
Humidity	?	x	x	x	x	x	x	x	x	x	x
<b>OTHER</b>											
Restricted entrance				x				x <sup>b</sup>	x <sup>b</sup>	x	
Dazzle, light physiology						x					

<sup>a</sup> If supplemented with host or CO<sub>2</sub>.

<sup>b</sup> In some designs.

? Possible.

upon the structure of the house, while the technique used to effect mosquito capture and the numbers of shelter-seeking mosquitoes present will affect the physiological composition.

Ramp traps are large traps which face in one direction, the ramp guiding approaching mosquitoes upward and through a narrow slot at the top into a cage. While the trap itself is unbaited, they have commonly been used at various distances from a bait to determine the distance of attraction (Gillies 1969, Gillies and Wilkes 1969, Edman 1979). Visual responses to the traps are evident, as shown by the larger catches taken in the more visually conspicuous traps when left unbaited (Gillies and Wilkes 1974, Edman 1979). Because of the narrow opening into the collection chamber, the number of species taken is small.

Gravid females of species that oviposit in small containers can be taken by mounting a miniature suction trap just above the water's surface (Reiter 1983). Using water with an organic infusion as the attractant, the traps have been successfully used for *Culex* females.

**MEASURING POPULATION CHANGES**

**THE SAMPLING SITE.** Because of mosquito responsiveness to terrain features and weather, considerable differences in population densities often occur within even short distances. Any proposed sampling site should be assumed to be less than ideal and occupied by a smaller population than would occur in a perfect site. The sampling site needs to be chosen according to the preferred flight habitat of the target species. For females of woodland and field species,

the selection of a trap site in woodland and field, respectively, would be most productive. For commuter females, a field trap site should be chosen, but close to the woodland that provides daytime resting sites. The skyline of the woodland should be at an approximate angle of about 30°-45° as seen from the trap site (Bidlingmayer and Hem 1981). This location would be equally suitable for females of field species also.

Although traps sample only those mosquitoes in their immediate vicinity, their catches are intended to represent the mosquito population over a much greater area. Therefore, the trap site should not be atypical of the area it is supposed to represent. Sites near intensive mosquito breeding, concentrated blood sources, large commercial or industrial developments or with other unusual characteristics, should be avoided.

Trap sites beneath a forest canopy are little affected by lunar illumination (Bidlingmayer 1967). Trap sites beneath isolated trees will probably be areas of low mosquito numbers; suction trap catches of field and commuter species beneath a large horizontal net were only 10-40% as great at new moon and 20% to 70% as great at full moon, as catches from traps in the open field (Bidlingmayer 1975). Catches of woodland females, such as *Cx. nigripalpus* and *Cs. melanura*, however, were only slightly affected.

Of all meteorological factors, wind is the most variable between sites. Trap sites should be selected, as far as possible, to be equally protected in all directions from wind. This is difficult where large numbers of traps must be placed, but trap protection during the mosquito

season is most needed from the prevailing winds.

**SELECTION OF A SAMPLING TECHNIQUE.** Because of biological and environmental factors, an unbiased sampling technique for adult mosquitoes does not exist. Table 1 summarizes, for each method, the kind of flight sampled and the meteorological and behavioral factors that affect the numbers and composition of the collection.

Disregarding stationary nets used to sample migrating mosquitoes, the truck trap, a non-attractant sampler, provides the least biased measure of appetential flight activity. Prior to the moment of capture, the population will have been affected only by meteorological factors. Wind direction is seldom of importance due to the usual variety of terrain features along the route and particularly if, midway during the run, the vehicle turns and retraces its route.

All other sampling methods are operated at fixed locations and therefore are vulnerable to changes in mosquito flight paths, which are dictated by changes in wind direction. Suction trap catches appear to be affected by a smaller number of variables than any other kind of fixed trap. The rotor trap may be comparable to the suction trap in this respect. Although mechanically more complex, because the nets sweep a wide area, the rotor trap may be less affected by minor shifts in mosquito flight paths. Malaise and light trap catches have been affected by mosquito behavioral and physiological responses, respectively, to trap design and mode of operation.

The responses of female mosquitoes to terrain and weather factors during consumatory flight can be expected to differ from those made during appetential flights. Because of the short range of olfactory attractants, mosquitoes first arrive near the trap site by one or more appetential flights and consequently the composition of the catches have been affected by the behavioral responses made during both flights.

Because mosquito numbers may range across 2 or 3 orders of magnitude, even unlike sampling methods may show similar population changes. However, while almost any technique may be used to measure population changes, each additional variable increases the difficulty of evaluating the catches. The greater the number of variables to which the catch has been exposed, the less representative the catch will be of the population. Although the numbers of females captured by attractant techniques may be large, the catches consist primarily of females in one gonotrophic stage. The preferred

sampling method for population measurement is not necessarily the method that takes the largest numbers. The sample should be adequate for statistical analysis while having been affected by the least number of variables. In Florida, truck and suction traps have been more satisfactory for conducting mosquito studies than have other methods. Except for the large manpower and vehicle requirements, the truck trap clearly would be the method of choice for most species.

**METEOROLOGICAL EFFECTS UPON CATCHES.** The effect of meteorological factors upon mosquitoes differ from other factors, as habitat, physiological needs and terrain features, in that mosquitoes cannot fly elsewhere and find more favorable conditions. If temperatures fall, it becomes cold everywhere, if winds increase, wind velocities increase everywhere. Frequent meteorological changes are the cause of much night-to-night variability in mosquito collections. If the influence of meteorological factors upon flight activity could be assessed, collections could be adjusted to offset their effect.

**ILLUMINATION.** Unlike temperature, wind, or humidity, illumination is independent of other meteorological factors. Twilight illumination is due to sunlight refracted around the curvature of the earth by the earth's atmosphere. Moonlight is important only during the nocturnal hours, i.e., after the evening and before morning twilight. The amount of light from the stars is negligible (.001 lux), but near urban areas illumination from city lights reflected downward from low clouds may be appreciable.

*Twilight illumination.* The 2 principal characteristics of twilight illumination are the wide range in illumination levels that occur each day and the repetitiveness of the phenomena. Whether a mosquito is in an open field or beneath a forest canopy, the same range of intensities, from too high to too low for optimum flight, will be experienced. An account of twilight illumination has been presented by Nielsen (1963), who constructed tables of illumination levels in crep units (multiples of civil twilight) for the sun at various elevations above or below the horizon. The presence of clouds near the horizon may either increase or decrease illumination from the tabular values but, due to the rapidity of illumination changes at twilight, in numerous observations the error was < 5% (Nielsen and Nielsen 1963). In Florida, with relatively short twilights, the illumination an hour after sunset is < 1/1000 that at sunset.

When 4 truck trap collections were made at equal time intervals during an 80-90 min period after sunset (until astronomical twilight),

about 92% of all mosquitoes captured were taken in the 2 center collections (Bidlingmayer 1974). The illumination levels at these times were 8.5 and 0.13 lux, (0.95 and 1.66 crep), respectively. Only 1% were taken in the first collection after sunset while numbers captured during the last collection varied according to the amount of moonlight present. An evening collection should embrace the period between sunset and 2.0 crep. The pattern of catches before dawn were essentially a mirror image of evening catches although the numbers captured were smaller.

**Nocturnal illumination.** Full moon illumination is 0.2 lux, which falls within the range of twilight illuminations during which mosquitoes were most active. However, flight activity during the nocturnal period on full moon nights was only about half as great as during the peak of activity during twilight (Bidlingmayer 1966), which may indicate that half of the night is spent resting. At first and last quarter moon, illumination is only 0.02 lux, and furthermore, the moon is in the sky for only half of the night. The amount of available moonlight, after factoring in the amount of lunar illumination and considering the elevation of the moon above the horizon, and the hours of duration for each day of the lunar cycle, is shown in Fig. 4. New moon equals 0% lunar illumination and full moon equals 100% (Bidlingmayer 1967). Although

first and last quarter moon phases (days 7.5 and 22.5) do not actually have the same illumination values, these differences are small compared to other sources of sampling error. The figure shows that, for the period new moon  $\pm$  3 days, total moonlight is  $<$  1% of full moon value. Thereafter, the amount of moonlight increases, first slowly than ever more rapidly until 2 days before full moon, i.e., until day 13. For more detailed information on lunar illumination and insect activity, see Muirhead-Thomson 1940, Bidlingmayer 1964, 1974, Bowden 1973, Bowden and Morris 1975.

Truck, suction and bait trap catches (the latter trap a modified Lumsden trap) were made for 3 consecutive days centered on the nights of new, first quarter, full, and last quarter moons (Bidlingmayer 1974). The effect of moonlight upon mosquito flight activity was measured by determining, for each moon phase, the percentage of the entire night's catch that was taken during the nocturnal periods, the 2 twilight period catches being only slightly affected by moonlight. For all species, the greatest increase in flight activity occurred during full moon with a lesser increase during the moonlit halves of quarter moon nights.

As the flight activity responses of *Ae. taeniorhynchus* to moonlight in both suction and bait traps were found to be similar,—and the same finding was true for *Cx. nigripalpus*—a regression equation was calculated for each species relating all night quarter and full moon catches with the percentage of available moonlight (Fig. 4). Although *Ae. taeniorhynchus* was about twice as responsive to moonlight as *Cx. nigripalpus*, extrapolation of their respective regression lines indicated both lines could be based on day 3 (or 27). This is not surprising, since the amount of lunar illumination on these nights does not differ essentially from day 0. Consequently, in the following analysis, the new moon trap data were assigned an age of 3 days. Both quarter moons (days 7.5 and 22.5) were assigned an age of 7.5 days and full moon an age of 14.5 days and a regression of catches on moon age calculated for each species.

Table 2 shows the percentage increase in collections taken at quarter moon and at full moon per trap night (twilight catches included) when compared with new moon catches. For most species, the percentage increase in catches between days 3 and 14.5 was about 2%–3% daily. The suction trap data appears to be less variable than bait trap data. The amount of error in assuming linearity between catches and moon age for *Ae. taeniorhynchus*, *Cx. nigripalpus*, *Ps. columbiae* and *Ae. vexans* (suction trap only), is probably small.

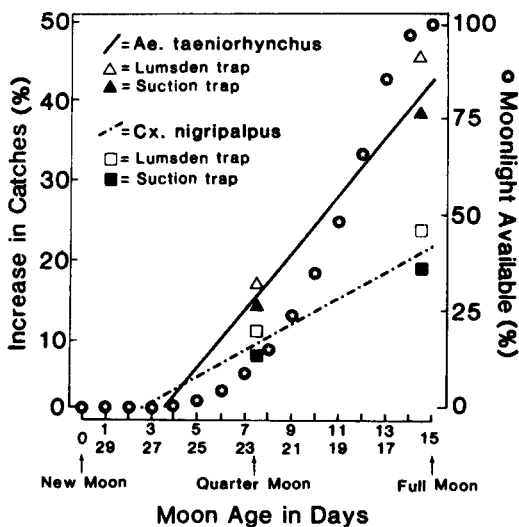


Fig. 4. Percent increase in suction and Lumsden trap catches of female mosquitoes taken at quarter moon and full moon above new moon catches. Amount of lunar illumination for each night is shown as a percentage with full moon illumination = 100%.

Table 2. Percent increase in mosquito catches (Y) per trap night above new moon catches for days (X) 3 (new moon), 7.5 (first and last quarter moon), and 14.5 (full moon), taken in suction and bait (Lumsden) traps (Bidlingmayer 1974). Also shown is the percent increase in daily catch with increasing moonlight between day 3 (or 27) and full moon.

Species	Moon phase				% daily increase
	N	Q	F		
SUCTION TRAP					
<i>Aedes taeniorhynchus</i>	0	13	38	$Y = 3.328X - 10.730^*$	3.3
<i>Aedes taeniorhynchus</i> <sup>a</sup>	0	6	14	$Y = 1.238X + 38.702^{**}$	1.2
<i>Psorophora columbiae</i>	0	13	37	$Y = 3.236X - 10.298^*$	3.2
<i>Aedes vexans</i>	0	13	42	$Y = 3.695X - 12.457$	3.7
<i>Culex (Melanoconion)</i>	0	8	45	$Y = 4.023X - 15.935$	4.0
<i>Culex nigripalpus</i>	0	7	18	$Y = 1.566X - 4.715^{**}$	1.6
<i>Culex nigripalpus</i> <sup>a</sup>	0	8	21	$Y = 1.792X + 46.782^{**}$	1.8
<i>Culex nigripalpus</i> <sup>a, b</sup>	0	0	0	$Y = -0.029X + 40.813$	0.0
BAIT TRAP					
<i>Aedes taeniorhynchus</i>	0	16	45	$Y = 3.933X - 12.442^*$	3.9
<i>Psorophora columbiae</i>	0	11	35	$Y = 3.077X - 10.308$	3.1
<i>Aedes vexans</i>	0	3	-15	—	—
<i>Culex (Melanoconion)</i>	0	24	24	—	—
<i>Culex nigripalpus</i>	0	10	23	$Y = 1.988 - 5.563^*$	2.0

\* P = <0.05.

\*\* P = <0.01.

<sup>a</sup> Data from Bidlingmayer 1967.

<sup>b</sup> Trap located beneath forest canopy.

The increased catches of mosquitoes due to moonlight in truck trap collections were several times greater than was found in the suction or the bait trap (Bidlingmayer 1974). This difference is probably due to the truck's mobility and its freedom from the effects of physical features about a fixed trap site. Although taking all night catches routinely seems impractical,

information is available on the effect of differing levels of lunar illumination upon truck trap catches during various periods of the night (Bidlingmayer 1964, 1966, 1974).

In contrast to truck, suction, and bait traps, New Jersey light trap collections were smaller at full and quarter moons than at new moon. Field data (Bidlingmayer 1967) indicated that moon-

Table 3. Mean numbers of female mosquitoes captured per trap night in the New Jersey light trap at moon ages from 6 to 24 days showing percent decrease per day in catches as moon waxes. Trap data transformed to logarithms for regression analysis (N = 19).

Moon age	<i>Aedes taeniorhynchus</i>		<i>Culex nigripalpus</i>		<i>Culex nigripalpus</i> <sup>a</sup>	
	Nos.	Log	Nos.	Log	Nos.	Log
6, 24	61.0		4.7		24.3	
7, 23	50.7		4.3		21.9	
(Quarter Moon)						
8, 22	49.0		4.0		21.1	
9, 21	49.5		3.8		20.6	
10, 20	36.3		3.5		20.2	
11, 19	28.2		3.4		18.6	
12, 18	24.0		2.3		19.5	
13, 17	20.2		2.2		19.3	
14, 16	15.8		1.7		18.4	
FM 15	17.0		1.6		18.2	
Y =	$-0.071X + 2.245^{**}$		$-0.054X + 1.041^{**}$		$-0.012X + 1.431^*$	
% decrease per day	15.1		11.7		2.7	

\* P = <0.05.

\*\* P = <0.01.

<sup>a</sup> Trap located beneath forest canopy.

light had little effect upon catches for about 5 days on either side of new moon. Table 3 shows the mean numbers of mosquitoes captured in a New Jersey light trap for days 6 through 24. In the table the numbers taken on the 9 days, with comparable illumination levels, on either side of full moon are averaged for easier comparison. Transforming the mean catch for days 6–24 (N = 19) into logarithms prior to analysis improved linearity of the data. For *Ae. taeniorhynchus*, the anti-logarithm of the regression coefficient,  $-0.0712$ , i.e.  $0.849-1.0 = -0.151$ , indicated that between day 6 (or 24) and day 15, catches declined 15.1% from each preceding day. Conversely, catches would need to be increased 17.8% from each preceding day for catches made on moonlit nights to be equal to dark nights. Catches of *Cx. nigripalpus* at Vero Beach and Myakka declined 11.7% and 2.7%, respectively, from each preceding day's catch.

Catches of *Ae. taeniorhynchus* were 4 times, and *Cx. nigripalpus* 3 times, greater near new moon than at full moon. Due to reduced moonlight penetration, light trap catches taken beneath a forest canopy were only 28% greater at new moon than at full moon.

TEMPERATURE. As morning temperatures were usually lower than evening temperatures, the effect of temperature upon mosquito flight activity was studied by comparing the numbers captured by the truck trap during evening and morning twilight periods on those nights when all evening temperatures were  $\geq 22^\circ\text{C}$  (Bidlelingmayer 1974). Evening catches were compared with morning catches when morning temperatures were  $\geq 22^\circ\text{C}$ ,  $21^\circ-19^\circ\text{C}$ ,  $18^\circ-16^\circ\text{C}$  or  $< 16^\circ\text{C}$ . There were no significant differences in the size of morning catches of any species when morning temperatures were either  $\geq 22^\circ\text{C}$  or  $21^\circ-19^\circ\text{C}$ ; therefore, temperature  $\geq 22^\circ\text{C}$  were greater than the upper threshold. Nights with all temperatures  $\geq 22^\circ\text{C}$  could then be deleted. Except for *Ae. vexans*, the upper temperature threshold for all species was within the range of  $21^\circ-19^\circ\text{C}$ .

Truck trap catches of *Cx. nigripalpus* were

compared with the midpoint temperature of each temperature class, i.e.,  $20^\circ\text{C}$ ,  $17^\circ\text{C}$ , and  $14^\circ\text{C}$  representing the classes  $21^\circ-19^\circ\text{C}$ ,  $18^\circ-16^\circ\text{C}$ , and  $< 16^\circ\text{C}$ , respectively. The percentage taken in the morning of the total numbers captured in both evening and morning, were 87%, 47% and 14% when morning temperatures were  $20^\circ$ ,  $17^\circ$  and  $14^\circ$ , respectively. Morning catches are expressed as ratios in Fig. 5 (87/87, 47/87, 14/87). The regression equation indicates that, for each  $1^\circ\text{C}$  decrease in temperature below  $20^\circ\text{C}$ , there was a 14% decrease in the catch. This procedure was also applied to other species (c.f. Table 4).

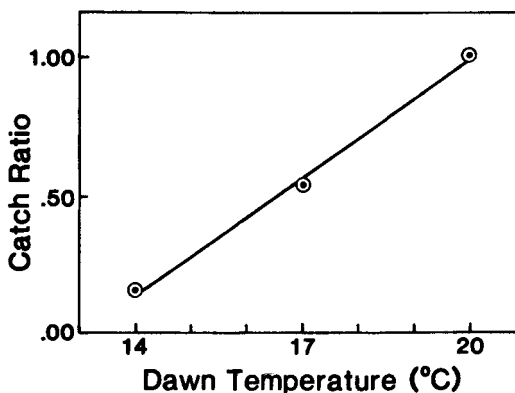


Fig. 5. Ratio of morning to evening truck trap catches of female *Culex nigripalpus* when all evening catches were taken at temperatures  $\geq 22^\circ\text{C}$  and morning temperatures were as shown. For details, see text.

The decrease in mosquito numbers with falling temperatures was quite similar for most species, ranging between 12% and 14% for each  $1^\circ\text{C}$  decrease (Table 4). The temperature at which appetential flight ceases is difficult to determine directly, due to the small numbers in flight when temperatures are very low. These equations indicate that in Florida the lower temperature threshold for flight is about  $12^\circ\text{C}$  or  $13^\circ\text{C}$ .

Table 4. Percent decrease found in truck trap catches of mosquitoes with each decrease of  $1^\circ\text{C}$  below an upper threshold temperature of  $20^\circ\text{C}$  (mid-point of range  $19^\circ\text{C}-21^\circ\text{C}$ ).

Species	Percent decrease	Estimated lower threshold	
<i>Culex nigripalpus</i>	14	$13^\circ$	$Y = .140X - 1.813^*$
<i>Aedes taeniorhynchus</i>	13	$13^\circ$	$Y = 0.133X - 1.710$
<i>Aedes sollicitans</i>	12	$12^\circ$	$Y = 0.118X - 1.392$
<i>Culex (Melanoconion)</i>	13	$12^\circ$	$Y = 0.127X - 1.580$
<i>Psorophora columbiana</i>	14	$13^\circ$	$Y = 0.138X - 1.802$
<i>Aedes vexans</i>	(see text)		

\*  $P = < 0.05$ .

The upper and lower threshold temperatures represent the limits of a normal curve and a mean threshold temperature would lie about midway. Thus, within this temperature range, a sigmoid curve would more accurately represent flight activity at each temperature. However, when limited to 3 pairs of data points, only a linear relationship may be described. Considering the many other factors that affect trap catches, for the present a linear representation of flight activity should be adequate.

For *Ae. vexans*, the upper threshold temperature was 18°C–16°C, as there were few differences among morning/evening catch ratios for these temperature classes  $\geq 22^\circ\text{C}$ , 21°C–19°C, or 18°C–16°C. Catches made when morning temperatures were  $< 16^\circ\text{C}$  were 70% as great as catches made at 17°C—a decline in catches of 30% when temperatures fell 3°C. Extrapolation of a 10% decline per degree implies a lower threshold temperature of about 7°C, which seems unreasonably low. Should the minimum threshold of this species be about 12°C, and the 30% decrease observed in flight activity represent only the upper arm of a sigmoid curve, the rate of decreased flight activity through the central portion of the curve must be precipitous indeed. The lower temperature threshold of this species probably lies between 7°C and 12°C.

**WIND.** All wind velocities are mean velocities; during any time period, whether a night, an hour, or a few minutes, wind velocities are inconstant. The effects upon mosquito flight of 2 winds with the same mean but differing ranges of velocities, may not be inconsiderable, particularly if some velocities overlap flight thresholds.

Trap catches of Florida mosquitoes taken at differing wind velocities were reported in 3 studies (Bidlingmayer 1967, 1974, Bidlingmayer et al. 1985). During the 1967 and 1974 studies, the traps were located about 18 m from an anemometer. The trap sites were situated among dense shrubs, many exceeding the height of the traps, as well as a few scattered short trees. Suction, New Jersey light, and bait trap collections were taken at several points along a perimeter about 18 m from the anemometer. Truck trap catches were made along the adjacent highway. The elevation of the anemometer was approximately the same height as the taller shrubs. In the 1985 study, 2 suction traps were placed on a raft anchored in a large borrow pit. The anemometer was located at the leading edge of the raft, slightly above the elevation of the trap intakes.

There were several sources of error in these studies that reduce the reliability of the wind data. The anemometer was a standard instru-

ment and unresponsive to very low wind velocities. Consequently, on nearly calm nights the traps were probably subject to more wind than was recorded. Because the anemometer was operated at an elevation higher than the traps, actual wind velocities at the trap sites would be less than at the anemometer site. Furthermore, because of the irregularities of the vegetation canopy, wind direction changes would cause either traps or anemometer to receive varying degrees of protection from the wind. In contrast, the truck trap was exposed to much higher wind velocities than those at the fixed trap sites. Despite these difficulties, trap collections were markedly affected by differing wind velocities.

Suction trap collections of *Cx. nigripalpus* at differing wind velocities during the 3 studies are shown in Fig. 6. Mean wind velocities over 3 velocity ranges were examined with their associated trap catches, the catches being expressed as ratios. For example, in the 1967 study, wind velocity classes were  $< 0.04$ , 0.04–0.40, and  $> 0.45$  meters per second (mps). The midpoints of each class were 0.02, 0.22, and 0.63, mps. The mean numbers of mosquitoes captured at each velocity were 3.3, 1.7, and 0.7, respectively, i.e., a ratio of 1.00:0.52:0.21. These data—mean wind velocities and catch ratios—were plotted as shown (Fig. 6). The regression equation ( $Y = -1.215X + 0.929$ ), indicates that for each 0.1 mps increase in wind velocity, suction trap catches of *Cx. nigripalpus* decreased 12%. The same procedure was followed in the 1974 studies, the midpoints of the wind velocity classes being 0.22, 0.67, and 1.12. The decrease

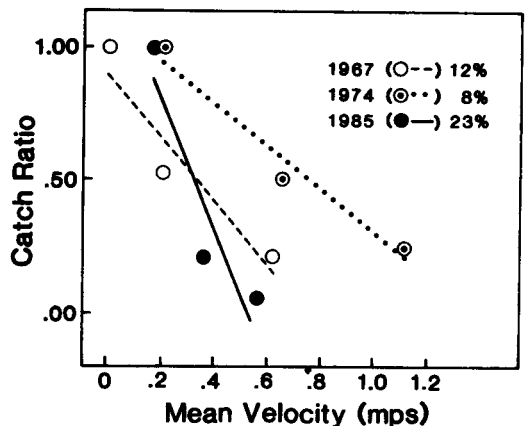


Fig. 6. Suction trap catches of female *Culex nigripalpus* with the mean catch taken at the lowest wind velocity within each study = 1.00, and mean catches at higher velocities as shown. Percent decrease in catch with each 0.1 mps increase in wind velocity is shown for the 3 studies.

in trap catches with each 0.1 mps increase in wind velocity was 8%.

Wind velocity classes during the 1985 study were 0.00–0.09, 0.10–0.24, 0.25–0.49, and  $\geq 0.50$  mps. Catches for the 2 lowest velocity groups did not differ significantly between groups for any species and therefore velocities between 0.00 and 0.24 mps were below the threshold for wind effects. Catches made at wind velocities  $< 0.10$  mps could therefore be eliminated from further analysis. The mid-points of the remaining classes, i.e., 0.10–0.24, 0.25–0.49, and  $\geq 0.50$  mps, were 0.17, 0.37, and 0.57, respectively. Catches taken at these velocities were expressed as ratios, with the numbers captured at the velocity of 0.17 mps as equal to 1.00. The regression equation indicates that, for each 0.1 mps increase in wind velocity, catches of *Cx. nigripalpus* were decreased 23% and of all species, 20%. The 1985 values seem suspect because, with a lower threshold velocity of about 0.2 mps, flight activity should cease at about 0.7 mps, a velocity well below mosquito flight speeds. As mosquitoes progressively reduce flight elevations as wind velocities increase, the relatively high vertical dimensions of the traps on the raft compared with their horizontal dimensions, together with the complete lack of adjacent visual features, may have encouraged mosquitoes to fly around the traps rather than over them. This would cause a more precipitous decline in trap catches than was occurring in flight activity.

This analysis was extended to collections of other species and to other sampling methods. Table 5 shows the percent decrease in trap catches due to increasing wind. Several points are evident: 1. For all traps and for all species, an increase in wind velocity as small as a tenth of a meter per second caused a noticeable de-

crease in trap catches. 2. Even though the trap sites were unchanged, the reduction in trap catches was greater in 1967 than in 1974. It is tempting to speculate whether increased vegetation height due to growth during the intervening period was the cause. 3. The greatest decrease in trap catches with increasing wind velocities was found in the 1985 study. Only in this study was the anemometer so placed as to measure wind velocities at the trap site. Due to wind protection afforded by the surrounding vegetation, the values obtained in 1967 and 1974 may be underestimates. 4. The catch reduction of only 2% obtained by landing rate counts may be due to mosquitoes following the collector as he walked to the site. 5. The catch reductions found for the truck trap, despite its undoubted exposure to winds much greater than those used in this analysis, were very similar to the catch reductions in the concurrent suction, New Jersey light trap, and the 1974 bait trap collections. This suggests that the effect of wind velocity upon trap catches is essentially linear and without an upper threshold. 6. The 1985 study suggests that 0.2 mps may be the lower threshold for wind influence upon flight activity.

The principal effects of wind direction upon trap catches will be determined by the characteristics of terrain features near the trap site. Obviously these will differ at each site. Terrain features may either expose or protect the trap from the wind.

**HUMIDITY.** Humidities near dawn are usually high but in the evening humidities have a much greater range. Bidlingmayer (1974) compared crepuscular suction trap catches of mosquitoes taken during the evening with those from the following morning with the difference between their relative humidities. Only catches taken on

Table 5. Percent decrease found in suction, truck, New Jersey light, and bait trap catches of mosquitoes taken during the years 1967, 1974 and 1985, with each increase of 0.1 mps in mean wind velocity.

Species	Suction trap			Truck trap		New Jersey Light		Bait trap*	
	1967	1974	1985	1967	1974	1967	1974	1967	1974
<i>Culex nigripalpus</i>	12	8	23	11	9	11	11		10
<i>Aedes taeniorhynchus</i>	11	9		12	10	7	9	2	9
<i>Psorophora columbiae</i>		9			8		6		
<i>Aedes sollicitans</i>					10				
<i>Culex erraticus</i>			21						
<i>Culex pilosus</i>			20						
<i>Uranotaenia sapphirina</i>			20						
<i>Anopheles crucians</i>			22						
<i>Mansonia titillans</i>			14						
Means:	11.5	9.0	20.0	11.5	9.0	9.0	8.7	2	9.5

\* Landing rate count in 1967; Lumsden bait trap in 1974.



nights with temperatures  $\geq 19^{\circ}\text{C}$  and winds  $< 0.4$  mps were analyzed. The analysis showed that, if dawn humidities were  $< 5\%$  greater than the preceding evening humidity, morning catches of *Cx. nigripalpus* were 28% as great as the evening catches; if dawn humidities were 5%–11% greater, morning catches were 33% as great, and if dawn humidities were  $> 11\%$ , morning catches were 44% as great as the evening catches. Assuming 2%, 8% and 14% represent the midpoints of the ranges  $< 5\%$ , 5%–11% and  $> 11\%$ , respectively, these data are shown as ratios in Fig. 7 (i.e., 28/28, 33/28, 44/28). The regression coefficient indicates a 4.8% increase in morning catches of *Cx. nigripalpus* for each 1% increase of dawn humidities above evening humidities. The truck trap—exposed to higher wind velocities than the suction trap—data indicated a 3% increase in catches for each percent increase in dawn humidities, whereas the New Jersey light trap indicated a 19% increase! The latter result is probably an artifact as, unlike suction and truck traps, the New Jersey light trap captures larger numbers of mosquitoes during the dawn period than at dusk.

Except for larger catches by the New Jersey light trap of *Ae. vexans*, no other mosquito species in this study showed a similar relationship with humidity. However, the largest truck trap catches of both *Cx. nigripalpus* and *Ae. vexans* were usually taken during or immediately following a rain.

The preceding analyses compared evening and morning catches only. Assuming humidity changes between dusk and dawn were linear, for all night catches the percent increase for suction catches of *Cx. nigripalpus* would be only

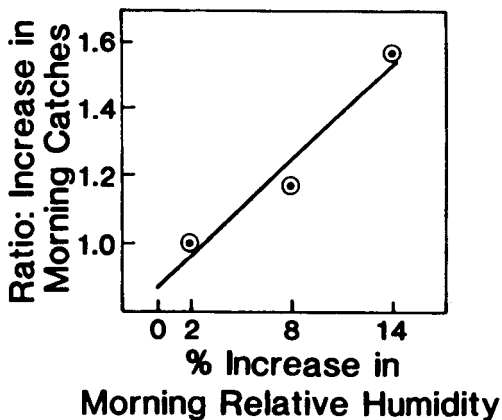


Fig. 7. Increase in morning suction trap catches of *Culex nigripalpus* with increasing levels of relative humidity above evening humidities. For details, see text.

half as great as indicated, i.e., a 2.4% increase in catch for each 1% increase in relative humidity between dusk and dawn. Dow and Gerrish (1970) had found a 3.6% increase in bait trap catches of this species with each 1% increase in humidity (measured 1 hr after sunset) from the preceding day.

The flight activity of *Ae. vexans* and many other species is probably affected by humidity levels, but the data are difficult to quantify. Other authors have noted that for some species very high humidities reduce activity, and therefore, the limitations of a simple linear relationship is obvious.

Illumination excepted, meteorological factors are interrelated. Due to increased radiation when the sky is clear, calm nights may be cooler but more humid than cloudy nights. Windy nights, because of disruption of the inversion layer, may be warmer but drier than calm nights. Thus the influence of one weather factor upon mosquito flight activity may be offset or reinforced by another.

## DISCUSSION

The pertinent features of mosquito behavior and ecology have been presented to emphasize that mosquito populations and flight activity are greatly affected by many factors. As a consequence, the mosquitoes comprising the collection are as much a reflection of the features of the trap site and the weather as of the size of the population. From this it may be concluded:

(1) All trap sites are unique. Due to a site's physical characteristics and its location in respect to the proximity of physiological needs and alternate habitats, the quality of each site as a mosquito habitat differs from all other sites. Consequently, each trap site has a mosquito population that is also unique, both as to species and physiological composition. That some trap sites consistently produce larger or smaller catches than other sites, is a common experience. If each site's population is unique, little can be learned by directly comparing the numbers captured at one site with those at a distant site, if the objective is to monitor population changes. Population changes should be monitored at each site by determining the difference between the most recent catch and earlier catches.

(2) It is seldom realized how rarely meteorological conditions do not, in some way, depress mosquito flight. Illumination is usually suboptimal as full moon occurs once monthly; in central Florida nights with temperatures  $< 19^{\circ}\text{C}$  occur during 7 months of the year; winds  $> 0.24$  mps are common throughout the year

and, except in summer, humidities > 90% occur only during the last hours of the night (unpublished data). On nearly all nights, flight activity will have been moderately to severely depressed by adverse meteorological factors.

**ASSESSMENT OF POPULATION CHANGES.** To adjust mosquito catches to compensate for meteorological effects, weather conditions during the night of the catch must be known. In the following example it is assumed that a suction trap, located in an open field, captured 10 specimens of *Cx. nigripalpus* on day 9 (moon age). The weather data for the night showed the mean temperature was 18°C, the wind averaged 0.4 mps and the relative humidity increased 7% between dusk and dawn.

The first step is to reduce the catch to the numbers that would have been taken without the presence of moonlight. Table 2 shows, for *Cx. nigripalpus* captured in a suction trap in an open area, 1.6% and 1.8%, increase in catch per day from new moon (day 3). Using 1.7% (p) per day for the 6 days (n) between days 3 and 9 as an average value, catches were 10.2% greater on day 9 than if moonlight had been absent. Thus, in this example the moonlight correction factor (k) is  $k = 1 - (np/1-np) = 0.89$ .

The hourly temperature record for the night should be examined for any periods of time below 19°C. Because this temperature is an upper threshold and higher temperatures do not increase flight activity, the mean temperature for the night is determined by recording all temperatures of 19°C or greater as 19°C. Table 4 shows truck trap catches of *Cx. nigripalpus* declined 14% (p) for each degree (n) the mean is below 19°C. In this example the correction factor (k), for 1°C below the upper threshold temperature, is  $k = 1 + (np) = 1.14$ .

Table 5 shows the values that were obtained for the percent reduction of trap catches due to wind with each increase in velocity of 0.1 mps. As discussed previously, there are reasons to believe the 1967 and 1974 values may be too low and the 1985 values too high. In all 3 studies, there was little difference between species within years. If a decrease of 14% (p) for each increase of 0.1 mps in mean wind velocity (m) above a threshold of 0.2 mps is selected as a compromise value for *Cx. nigripalpus* in this example the correction factor (k) for wind velocity is  $k = 1 + (m-0.2) (10p) = 1.28$ .

Suction trap catches of *Cx. nigripalpus* during the dawn period were 4.8% (p) greater than expected for each 1% increase above evening relative humidities (Fig. 7). Assuming the increase in humidities between dusk and dawn was linear, the increase in catches for the entire night would be ½ that, or 2.4% per night for each 1% difference (n) between dawn and dusk

humidities. Therefore, the correction factor (k) would be  $k = 1 + (p/2)n = 1.17$ .

Since, in this example, the suction trap had captured 10 mosquitoes, multiplying the trap catch by the product of all correction factors (1.52), indicates that the adjusted trap catch would be 15.2 mosquitoes for that night. Even though the given weather conditions were mild, the catch had been depressed by a third. The adjusted trap catch may now be added to all earlier catches at that site and a new mean and standard deviation (S.D.) determined. The deviation of the most recent night's catch from the mean of all earlier catches, is reported as the number of S.D., positive or negative, by which it differs from the mean. This procedure would evaluate population changes at each site independently of the numbers captured, e.g., a catch equal to 2.5 S.D. would indicate only 1 day in 100 could be expected to have a collection of that size. Population changes at one site would be directly comparable to those at all other sites.

Although indices between biting-landing rates and measures of flight activity may be similar, from an adultciding viewpoint flight activity is the more important measure as mosquitoes are most vulnerable when in flight. However, during the initial period of the surveillance program, landing or biting rates should be obtained within the area represented by each trap to establish an approximate relationship between the local level of annoyance and the trap's measure (in S.D.) of population changes. The number of positive S.D. required to indicate a need for control, however, will always remain an operational decision, as this will be based upon the mosquito control director's assessment of the need for control in that area.

A final point to be determined is whether the adjusted trap catches provide a better measure of an adult mosquito population than the original catch. While likely, the concept can only be tested in the field. To test this hypothesis, a grid of traps should be located adjacent to a principal breeding area of a floodwater mosquito. Trap spacing would depend upon the dispersal range of the target species. Following a large emergence, the outward movement of adult mosquitoes should show clearly if the adjusted trap catches are plotted on a map and isograms drawn to delineate areas of differing adult densities. The distribution gradients obtained with adjusted catches should show population changes more clearly than by the use of unadjusted catches. The application of meteorological correction factors to mosquito catches will be most effective for those sampling methods least affected by other variables.

If measuring changes in adult mosquito

populations is to become more of a science, it will be necessary to compensate for the variability in samples caused by biological and environmental factors. The effect of these factors upon mosquito flight activity and collections is too great not to be addressed. The proposed scheme has several weaknesses, e.g., the values used here for the effect of meteorological factors upon mosquitoes need considerable refinement, and furthermore, their relationships with mosquito activity are undoubtedly curvilinear, rather than linear. Nevertheless, a start must be made. To reach the goal of securing reliable samples, mosquito control districts may well lead the way. A well-designed sampling program, operated regularly over many seasons, would produce such a volume of data that the deficiencies just noted could certainly be greatly improved.

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